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CHELIPED LATERALITY IN *CALLINECTES SAPIDUS* (CRUSTACEA: PORTUNIDAE)

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In bilaterally symmetrical animals possessing paired appendages, the members of each pair are usually morphologically identical. This generalization holds true for crustaceans often postulated as being most similar in form to ancestral stocks. However, members of several reptantian decapod families (Nephropidae, Calappidae, Xanthidae, Portunidae, Gecarcinidae, Ocypodidae) possess dimorphic chelipeds in both sexes, each cheliped having a different function during feeding. Typically, one cheliped is larger and possesses large bluntly-tipped teeth (the major cheliped or crusher) and the other cheliped is smaller and possesses small sharply tipped teeth (the minor cheliped or cutter). Members of other reptantian families (*e.g.*, the Parthenopidae, Majidae) may also possess dimorphic chelipeds. However, it is unclear if these species possess true crusher and cutter chelipeds having different functions during feeding, and if the dimorphism exists in both sexes (see Vernet-Cornubert, 1957).

While cheliped laterality, or the location of the crusher and cutter chelipeds (sometimes called handedness), has been studied in the special case of male *Uca* spp. (Przibram, 1931; Vernberg and Costlow, 1966), laterality of reptantians having crusher and cutter chelipeds has rarely been examined. In a sample of 2430 *Homarus americanus*, Herrick (1909) found 1266 had a left crusher and right cutter, and 1164 had the opposite configuration. Although Herrick cites these results as evidence for a 1 : 1 ratio, we find his data significantly ($X^2 = 4.28$, $P < 0.05$) different from a 1 : 1 ratio. Przibram (1931) claimed that all Brachyura start out with a right crusher, and that reversal of this configuration in some crabs is caused by autotomy of the crusher. This conclusion was based on experiments with *Portunus corrugatus*, *P. depurator*, *Carcinus maenas*, and *Eriphia spinifrons*. However, subsequent researchers studying *Calappa* spp. (Shoup, 1968), *Portunus puber* (Ebling, Kitching, Muntz and Taylor, 1964) and *Carcinus maenas* (Seed, 1969) only state that "usually" or "normally" the crusher is on the right and the cutter is on the left. Schäfer (1954) illustrated the dimorphic chelipeds of many brachyurans, but did not state whether the cheliped configurations of the specimens illustrated were representative for the species. He did state that 8% of all *Portunus holsatus* lack the large tooth on the right cheliped, but was unclear whether this condition was due to excessive wearing of an otherwise normal crusher, or whether these crabs possessed two cutters. In 1601 *Neopanope texana sayi*, Swartz (1972) found that 79.9% had a right crusher (major cheliped) and left cutter (minor cheliped), 12.6% had the opposite configuration, 3.4% had two cutters and 4.0% were missing one or both chelipeds. He apparently did not consider a possible relationship between crab size and cheliped configuration, but did note that autotomy of the crusher did not cause reversal of the original con-

TABLE I

Collection data for the five Florida samples.

Sample location	Number	Collection date (1975)	Mean carapace length (±1 s.d.)
Gulf Coast			
St. Marks River (Wakulla County)	340	May 21	60.3 ± 5.80
Goose Creek Bay (Wakulla County)	181	May 26 to July 18	38.5 ± 8.70
Dickson Bay (Wakulla County)	274	August 4, 5	21.7 ± 8.04
Atlantic Coast			
Trout River (Duval County)	117	June 17	60.3 ± 5.54
Nassau Inlet (Duval County)	184	June 14	52.6 ± 5.95

figuration in 36 crabs maintained in the laboratory. The apparent rarity of specimens of *Calappa* with left crushers recently led to the erection of a new genus based on a single fossilized left crusher, which taxon was subsequently synonomized with *Calappa* after a more rigorous examination of the phenomenon of reversal (Lewis, 1969).

The apparent difference in cheliped laterality between macruran and brachyuran decapods was noted by Aristotle (quoted by Herrick, 1909), who wrote, "In the Caribi and in the Carcini the right claw is invariably the larger and stronger. In the Astaci alone it is a matter of chance which claw is the larger, and this in either sex."

Callinectes sapidus Rathbun possesses crusher and cutter chelipeds, with a large blunt tooth located proximally on the dactylus of the crusher of most individuals (see Williams, 1974, Fig. 16A). The chelipeds are used differently when feeding on the gastropod *Littorina irrorata* (Hamilton, 1976) and on the bivalve *Crassostrea virginica* (J. G. Halusky, unpublished observations). Williams (1974) states that the crusher and cutter of *Callinectes* are "usually" on the right and left, respectively, a few crabs have two cutters, and almost none have two crushers. However, he includes no quantification. Herein is presented laterality data based on six samples of *C. sapidus*, the possible sources of variation among samples are considered, and it is concluded that Przibram's (1931) aforementioned generalization holds for this brachyuran species.

MATERIALS AND METHODS

To quantify the incidence of crusher and cutter laterality in *Callinectes sapidus*, 1096 crabs from five different locations on the Gulf and Atlantic coasts of Florida,

USA were examined, along with 60 crabs hand-reared at the Duke University Marine Laboratory, Beaufort, North Carolina. Table I summarizes collection data for the five Florida samples.

Crabs from the St. Marks River, Trout River and Nassau Inlet were examined in processing houses after being trapped commercially. Crabs from Goose Creek Bay were netted in the upper intertidal zone during high tide. Crabs from Dickson Bay were either netted from a dock or captured in a shrimp trawl at night. The carapace length, sex and cheliped configuration was recorded for each crab examined in the five Florida samples. The crusher and cutter chelipeds of most crabs in these five samples were easily distinguished by the major dentition differences described by Williams (1974). However, the crusher dentition appeared considerably eroded in a few crabs, making them superficially appear to possess double cutters. Hence, extra care was taken when examining all crabs possessing similar chelipeds (double cutters or double crushers) to insure the accuracy of their identity. Only the position of the crusher and cutter chelipeds was recorded for the hand-reared sample, and this was determined solely by location of the large blunt tooth, using a dissecting microscope. Only crabs with two functional chelipeds were considered.

Results

Table II summarizes the data for all six samples. There was a significant ($X^2 = 61.8$, $P \ll 0.01$) difference among the five Florida samples for the incidence of the first two cheliped configurations in Table II. There was no significant correlation ($P > 0.3$ in each case using the X^2 test) between the first two cheliped configurations and sex in the St. Marks River, Goose Creek Bay, Trout River or Nassau Inlet samples, or when all five Florida samples were combined. While 14 of the 195 females in the Dickson Bay sample possessed a left crusher and right cutter, none of the 79 males possessed this configuration, making a X^2 comparison impossible for this sample. An analysis of variance showed significant [$F(4,1091) = 1416.3$, $P \ll 0.001$] differences in carapace length among the five Florida samples. The hand-reared sample was excluded from these statistical comparisons because of their extremely small carapace length (less than 5.0 mm), and because all individuals possessed the same cheliped configuration (crusher right, cutter left).

Although there was no clear relationship between carapace length and cheliped configuration in any of the samples when examined individually, there was a significant relationship when groups of samples were examined. Figure 1 shows the percentage (excluding crabs with double crushers and double cutters from the totals) of crabs in each size class with a right crusher and left cutter for different groups of samples. For the range of carapace lengths encountered in the three Gulf of Mexico samples (Fig. 1A) and in all six samples combined (Fig. 1C), there is a clear trend for the frequency of crabs with right crushers and left cutters to decrease as carapace length increases, and conversely for the frequency of crabs with left crushers and right cutters to increase. This trend is less clear in the Atlantic coast samples (Fig. 1B), probably due to the smaller sample sizes and narrower range of carapace lengths encountered. The fact that the hand-reared sample may

TABLE II

Cheliped configurations of 1156 Callinectes sapidus; (*L represents left*; *R*, *right*).

Sample origin	Crusher R cutter L	Crusher L cutter R	Cutter L and R	Crusher L and R	Totals
St. Marks River					
Males	148	55	12	0	215
Females	81	35	7	2	125
Total	229	90	19	2	340
Per cent	67.4	26.4	5.6	0.6	100.0
Goose Creek Bay					
Males	86	8	2	0	96
Females	71	11	3	0	85
Total	157	19	5	0	181
Per cent	86.7	10.5	2.8	0.0	100.0
Dickson Bay					
Males	71	0	6	2	79
Females	175	14	6	0	195
Total	246	14	12	2	274
Per cent	89.8	5.1	4.4	0.7	100.0
Trout River					
Males	46	9	10	0	65
Females	38	12	2	0	52
Total	84	21	12	0	117
Per cent	71.8	17.9	10.3	0.0	100.0
Nassau Inlet					
Males	35	4	14	0	53
Females	104	18	8	1	131
Total	139	22	22	1	184
Per cent	75.5	12.0	12.0	0.5	100.0
All Florida samples					
Males	386	76	44	2	508
Females	469	90	26	3	588
Total	855	166	70	5	1096
Per cent	78.0	15.2	6.4	0.4	100.0
Hand-reared					
Total	60	0	0	0	60
Per cent	100.0	0.0	0.0	0.0	100.0
All samples					
Total	915	166	70	5	1156
Per cent	79.1	14.4	6.1	0.4	100.0

have been the progeny of a single female, and probably experienced much less environmental stress than the five Florida samples, does not detract from the clarity of this relationship.

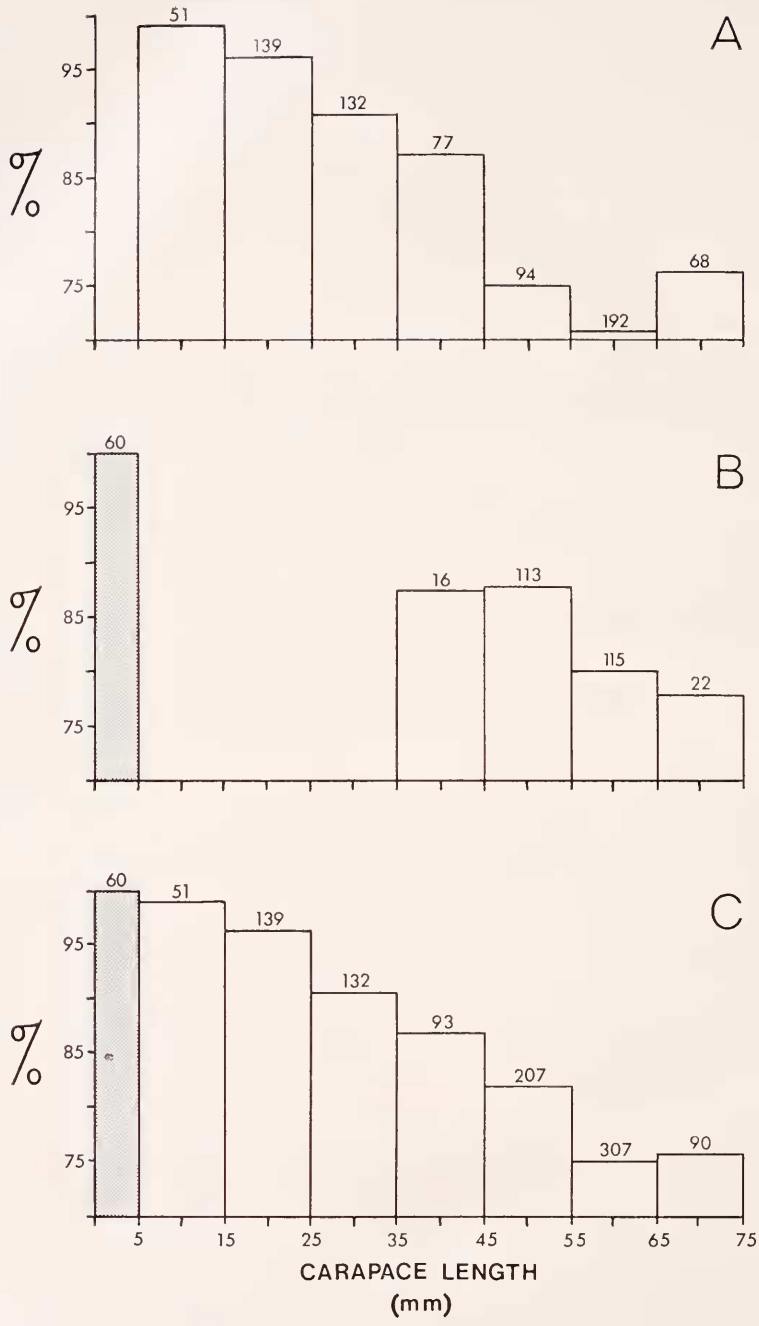
A multiple regression was run for the five Florida samples in an attempt to evaluate the effects of carapace length and sample location on cheliped laterality. However, due to the high correlation between carapace length and sample location, definite conclusions could not be drawn from this procedure.

In all 72 crabs from the five Florida samples which possessed a functional regenerated cheliped (determined by its qualitatively judged, relatively smaller size), that cheliped was a cutter. Twenty-six of these 72 crabs possessed a cutter on the opposite side from the regenerated cheliped (and hence possessed double cutters), and 46 had a crusher on the opposite side. Crabs having double cutters, one of which was regenerated, appeared significantly ($X^2 = 113.6$, $P \ll 0.01$) more often than would be expected if these two characters were not related. The fact that all 72 regenerated chelipeds were cutters suggests that double cutters actually result from the process of autotomy and regeneration. Crabs possessing double cutters, neither of which was identified as regenerated, probably commenced regeneration at an earlier date relative to their capture, and hence their chelipeds had grown more nearly identical in size. A crusher appeared on the opposite side from a regenerated cutter cheliped significantly ($X^2 = 5.56$, $P < 0.02$) more often than did a cutter.

Discussion

The data presented here suggest that some previous statements concerning cheliped laterality in *Callinectes sapidus* (and possibly in other brachyurans) have been somewhat oversimplified. The significant difference in frequency of the first two cheliped configurations among the samples could possibly be due to the different geographic locations where the samples were obtained; the significant differences in mean carapace length among the samples; or a combination of both factors. Discrete genetic differences among samples seem unlikely for several reasons. For example, the Gulf of Mexico samples were collected from closely located areas, with ample opportunity for unrestrained movement and gene exchange between adjacent areas, and for equitable settlement of pelagic larvae from parental sources. Tagging studies (Tagatz, 1968; M. Oesterling, University of Florida, personal communication) indicate that movements between the Atlantic coast sample locations, or among the Gulf coast sample locations, are well within the capabilities of adult crabs. Geographically related differences in the survival rate of crabs having different cheliped configurations could be responsible for the observed sample differences in cheliped laterality, but insufficient information is available to evaluate this possibility.

Figure 1 indicates that cheliped laterality is related to age, as indicated by carapace length, with all blue crabs apparently beginning life with a right crusher and left cutter. This trend is clear in the Gulf of Mexico samples (Fig. 1A), which almost certainly comprise a common gene pool. The observed decrease in the proportion of individuals with a right crusher and left cutter as crabs get older (larger) may be due to reversals caused by autotomy and regeneration, or merely due to spontaneous reversals at molting. Regardless of the mechanism responsible for this trend, future observations on cheliped laterality in brachyurans should in-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CARAPACE LENGTH
(mm)

clude consideration of possible ontogenetic differences in the frequency of a particular cheliped configuration.

The apparent direct relationship between the process of autotomy and regeneration and the incidence of crabs with double cutters has also been noted by Emmel (1907) in *Homarus*, and by Przibram (1931) in other brachyurans. However, the proportion of *C. sapidus* with double crushers or double cutters is much higher than in *Homarus*, where such individuals are quite rare (Herrick, 1909). The higher incidence of crabs with double cutters (and hence of autotomy and regeneration) in the Trout River and Nassau Inlet samples (Table II) is probably related to our observation that those crabs exhibited a higher frequency of cheliped damage and breakage than did crabs in the other samples.

The normal (and hence probably the most advantageous) cheliped configuration is undoubtedly one crusher and one cutter. However, in all 72 crabs possessing one functional regenerated cheliped, that cheliped was a cutter. This result certainly indicates definite selective advantage to regenerating a specific type of cheliped (a cutter) when either cheliped is autotomized. Since regenerating a cutter when a normal dimorphic crab autotomizes a cutter soon results in an almost normal crab, the selective advantage to always regenerating a cutter must accrue when a normal dimorphic crab autotomizes a crusher.

Przibram (1931) claims that a cutter is always regenerated so the crab can attain a full sized crusher and cutter again in the least amount of time. The original cutter only has to grow a little and undergo a change in dentition to become a crusher, and the regenerating cutter cheliped doesn't have to grow as much before it becomes a normal sized cutter. Since reversal of laterality is a major result in Przibram's theory, it also provides a mechanism for explaining the trend shown in Figure 1. Always regenerating a cutter regardless of which type of cheliped is autotomized could also be advantageous if spending some time with double cutters before reacquiring the dimorphism is not as disadvantageous as spending some time with double crushers. Examining the comparative versatility of crushers and cutters in feeding could provide insight into this theory. However, since a mechanism for reversal in laterality is not included in this theory, it is less parsimonious than Przibram's theory, which explains both phenomena. Neither theory accounts for the rare (0.4%) occurrence of crabs with double crushers.

Przibram (1931) also claims that complete reversal proceeds more quickly in smaller individuals of a species, and intermediate double cutter molt stages are more likely to occur in larger (older) individuals. Insufficient data is available to determine if a trend exists between the incidence of double cutters and carapace length in *C. sapidus*. However, the carapace lengths of the 70 crabs with double cutters were significantly ($z = 2.78$, $P < 0.01$) greater than those of the 1021 crabs with dimorphic chelipeds. If the incidence of double cutters is indeed

FIGURE 1. Relationship between carapace length and the percentage of crabs in each size class interval with a right crusher and left cutter for the three Gulf of Mexico samples (A), for the hand-reared sample and the two Atlantic Ocean samples (B), and for all six samples combined (C). Shaded area indicates the hand-reared sample in B and C. Crabs with double cutters or double crushers are excluded from the totals. The number of crabs in each size class interval is shown above each histogram bar.

greater in larger crabs, this may be partly due to a large cutter being able to produce enough force for most crushing tasks, making reacquisition of the dimorphism unnecessary.

The apparent reversal of laterality caused by autotomy of a crusher undoubtedly requires modifications in neural control of the chelipeds because of their different use during feeding. Regardless of whether such modifications involve actual nervous "rewiring" or merely relearning which cheliped is which, study of these changes would likely provide insight into the endogenous control of behavior in crustaceans. It would be most interesting to learn if blue crabs preferentially autotomize a cutter rather than a crusher in stressful situations. Such a response would presumably avoid a change in laterality, and would also be advantageous if a crusher is a more generally useful tool in feeding. Although crushers were found opposite regenerating cutters significantly more often than were cutters, this result could be due to either preferential autotomization of cutters, or (presuming Przibram's theory is correct) when a crusher is autotomized, to a change-over from the old cutter to a crusher before full size is attained by the regenerating cutter.

The difference in cheliped laterality between brachyuran and macruran decapods (if indeed one exists) may represent extant differences in selective pressure related to habits or habitat. Alternately, selective pressures leading to differences in laterality may only have existed in the past, and particular configurations may not provide any advantage in extant forms. Certainly the simplest explanation for the initial crusher location in brachyurans was advanced by Aristotle (quoted by Herrick, 1909), who wrote, "For it is natural to every animal to use its right side in preference to its left."

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Summary

Blue crabs from five locations on the Gulf of Mexico and Atlantic Ocean coasts of Florida, USA, and juvenile crabs reared in the laboratory, were examined for the incidence of cheliped laterality (location of the crusher and cutter chelipeds). The proportion of crabs possessing the crusher cheliped on the right decreased with size (age) from 100% in the smallest crabs to about 74% in the largest crabs. Crabs with two cutter chelipeds were not uncommon and apparently resulted from regeneration of a cutter regardless of which cheliped was autotomized. Only 0.4% of all crabs possessed two crusher chelipeds.

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